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Review of Forage Losses Caused by Rangeland Grasshoppers

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ABSTRACT

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Research studies on forage losses by rangeland grasshoppers have been reviewed. Factors that relate to forage losses are discussed (food preference, density, habitat, grazing influence, weather, human influence, and physiological influences). A listing is given of the most destructive rangeland grasshopper species, their area of potential damage, and their preferred food plants. Estimated amounts of forage lost are listed for populations and certain economic species. A means of predicting forage losses once certain information is obtained is suggested.

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Review of Forage Losses Caused by Rangeland Grasshoppers

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INTRODUCTION

Grasshoppers have been of economic concern on rangeland in the United States since 1877 when the Rocky Mountain locust, *Melanoplus spretus* (Walsh), damaged both crops and rangeland vegetation to the extent that the U.S. Entomological Commission was created by Congress to investigate the problem (Riley 1892).² Crop protection was the main concern of the early settlers, and only in more recent years have rangeland losses been of concern. Parker (1933) stated:

The control of grasshoppers on rangeland is a problem that is demanding attention. Forestry officials have complained that the grazing capacity of the national forests is being reduced by grasshoppers, and cattlemen in Texas have asked for help in protecting the extensive areas of rangeland in that state from the ravages of grasshoppers. In British Columbia grasshopper control on rangeland is more important than in cultivated crops.

Even as late as 1948, public interest generally was not focused on control of grasshoppers on rangeland (Wakeland 1951). However, grasshoppers have continued to be the most conspicuous and damaging insects on western rangeland.

According to Cowan (1958), damage to rangeland varies geographically and from year to year. It is governed largely by the grasshopper species complex, the vegetation complex, the numbers of grasshoppers, and the weather. Three types of damage are possible: (1) Removal of forage in direct competition with livestock, (2) permanent damage to the plants due to continued feeding by grasshoppers beyond accepted percent use factors, and (3)

destruction of seed heads, which prevents natural reseeding.

Newton and Esselbaugh (1952) stated that when grasshoppers feed on the top of plants they are consuming forage or browse in direct competition with livestock, and when they feed on plant material near the ground they are contributing to overgrazing and weakening the root reserves in the stand, and may possibly be making way for later soil erosion.

According to Parker (1937), undetermined costs associated with grasshoppers fall into two categories: (1) Losses of livestock, which includes animals that died as a result of the destruction of pastures by grasshoppers, animals that were marketed prematurely or moved to new pastures with additional expenses incurred as a result of grasshopper damage, and losses due to decreased output of livestock products due to grasshoppers and (2) indirect losses, which includes families receiving relief in grasshopper and drought areas and losses in revenue due to crop losses and land abandonment.

Spackman et al. (1966) reported on how to figure the cost of not controlling grasshoppers. If pasture is available, one may estimate the cost at going pasture rent prices. If pasture is not available, one may have to calculate the cost of hay plus the cost of feeding it. If additional pasture cannot be rented and hay is not available or the price of either rises to prohibitive levels, herd reduction may be the only answer. The effect of this drastic measure lasts longer than the source of the problem. This also results in area unemployment, which is multiplied in local businesses. The decision whether or not to control grasshoppers is often difficult to

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² The year in italic, when it follows the author's name, refers to Selected References, p. 16.

make. The following tabulation shows the benefits from spraying on two rangeland areas with different carrying capacities, using cost of hay for comparison.

Item	Cost of hay		
	\$22.22/t	\$27.78/t	\$33.33/t
Carrying capacity at 8 ha/AUM:			
Value per hectare	9.13	11.40	13.70
Less cost of control per hectare	1.88	1.88	1.88
Benefit from spraying	7.25	9.52	11.82
Carrying capacity at 12 ha/AUM:			
Value per hectare	6.08	7.60	9.10
Less cost of control per hectare	1.88	1.88	1.88
Benefit from spraying	4.20	5.72	7.22

This tabulation is based on an animal unit consuming 8 to 9 kilograms of dry feed per day. Pfadt (1949b) used similar reasoning to estimate that a savings of \$11.50 per hectare could be made by spending \$2.25 per hectare to kill the grasshoppers in Wyoming. He also pointed out that cattle and sheep have an increase in weight (gains) when they do not have strong competition for forage. A rancher may make plans to have his pasture moderately grazed by livestock, when in fact if it contained 18 grasshoppers per square meter, the grazing would be extremely heavy. Bullen (1966) mentioned that modern control methods are expensive, and to justify this expenditure or at least put it into economic perspective, it is necessary to evaluate the effect of grasshopper damage upon agricultural production and its consequent effect upon the

human economy of the infested area. The same author suggested that damage to grazing land is difficult to assess quantitatively and even when assessed, difficult to express in economic terms. In semiarid regions, yields may vary greatly from year to year and depend principally on rainfall. To evaluate the quantitative effect of grasshopper damage, it is necessary to forecast the yield. Bullen (1972) also stated that grasshopper injury becomes economic damage when the yield of the crop is adversely affected, quantitatively and (or) qualitatively. The assessment of such economic damage is no easy task, and many factors have a bearing on vegetation losses caused by grasshoppers in the Western United States.

In 1973, I searched for ways of determining actual forage losses caused by rangeland grasshoppers. The main objective was to predict early in the spring the forage losses that would occur in the summer and later on in the fall if grasshoppers were not controlled. I soon realized that many other researchers had approached the same problem, and information was widely scattered. I, therefore, reviewed the more important papers that contribute to this subject. Presented here is a brief evaluation of the factors that contribute to forage losses caused by rangeland grasshoppers and also results of some of the studies in terms of estimated amounts of forage destroyed by grasshopper populations and species. I hope that this review will be useful to other entomologists researching this problem and will benefit those agencies and individuals who must make decisions on economic control.

FACTORS AFFECTING FORAGE CONSUMPTION BY GRASSHOPPERS

Food Preference

More than 600 species and subspecies of grasshoppers are in the United States, many with specific food preferences. However, not all of the species are of economic concern since some never become abundant, others are restricted to isolated habitats, and a few may be classified as beneficial. For example, Ball (1936) claimed that out of 130 species of grasshoppers occurring in Arizona and 130 occurring in Colorado only 5 or 6 should be classified as injurious to crops, and scarcely a dozen

more should be listed as serious pests of rangeland vegetation.

A Kansas study (Jantz 1962) with *Melanoplus femur-rubrum* (DeGeer) concluded that this grasshopper is probably of more economic importance as a beneficial insect rather than harmful on rangeland; however, it was found to be a crop pest, particularly on alfalfa. Burkhardt (1959) suggested that chewing insects such as grasshoppers may effectively prune the plants, resulting in plants with increased vigor and growth. Anderson (1970) stated that clipping studies indicate, under certain

conditions, grasshoppers may be responsible for increases in forage production over a period of years. Mitchell and Pfadt (1974) pointed out that grazing insects such as grasshoppers influence aboveground plant productivity by producing unassorted organic litter (fecal production plus destroyed material). They estimated that 20 adult *Melanoplus sanguinipes* (F.) per square meter could produce 29 g/m² of unassorted litter over 3 weeks. Approximately the same amount was produced by 20 adult *Aulocara elliotti* (Thomas) per square meter and 10 *Melanoplus foedus* Bruner per square meter.

About half of some 187 grasshopper species occurring in California can be classified as rangeland species (Middlekauff 1958). Cowan (1958) reported about 60 species occurring in the United States as being economically important, with 5 attacking crops and 55 important on rangeland. Hebard (1938), on the basis of abundance, listed 17 species as injurious on pasture and rangeland in Oklahoma. Twelve species were reported as being the most destructive in Canada on rangeland during the 1930's when the Canadian prairies were in the midst of a widespread and intense drought (Gibson 1938). Parker (1952) listed 17 species as being abundant on rangeland in Montana, North Dakota, South Dakota, Nebraska, and Wyoming from 1936 to 1952. Parker (1954) also stated that 100 species feed on range vegetation. However, species present in a given location are never present in equal numbers.

Wilbur and Fritz (1940) found that in Kansas, grasshopper populations on the native prairie are characterized by the genera *Orphulella* and *Merimuria*. They reported that approximately 68 percent of adult grasshoppers collected were of 4 species while 16 of the species collected were represented by 5 or fewer specimens. Middlekauf (1958) studied grasshopper populations on two foothill sites in California and reported that four species were predominant. Buckell (1945) stated that in the 1943-44 grasshopper outbreak in British Columbia, one species, *Melanoplus sanguinipes*, was dominant and caused damage to forages with little aid from other species. Before the outbreak, *Cannula pellucida* (Scudder) was the main species of concern, but in just one year's time *M. sanguinipes* spread from its usual habitats and invaded the highest cattle range areas where it never before had been recorded in high numbers. However, as Parker (1954) pointed out, since as many as 20 species may be

found living together, nearly all range vegetation is subject to attack, despite the specialized feeding. Parker (1952) also mentioned that studies in Wyoming showed that populations build up through slight to moderate increases of most major species rather than by large increases of a few species.

Kelly and Middlekauf (1961) pointed out that *Discolesteira spurcata* (Saussure) should not be considered by itself as having significant economic importance in California but along with many other species adds its share to the damage caused to the rangeland each year. Along with other species, *D. spurcata* would make reseeding of more desirable grasses very difficult.

Several workers—Isely (1938), Herman and Eslick (1939), Anderson and Wright (1952), and Brooks (1958)—have noted food preferences for a number of rangeland species, mainly from observations. Other workers have determined the preferred food plants for a number of rangeland species based on crop analysis. Lambley (1967) and Campbell et al. (1974) noted food preferences for Kansas grasshoppers. Hansen and Ueckert (1970), Ueckert and Hansen (1971), Ueckert (1968), and Ueckert et al. (1972) reported on food preferences for some Colorado grasshoppers. Mulkern et al. (1969) listed the food preferences for grasshoppers in North Dakota, Kansas, and Nebraska. In Idaho, Brusven and Lambley (1971) and Banfill and Brusven (1973) used crop analysis to determine the food habits and preferences of several important rangeland species. Gangwere (1961) has published the most complete study on food selection by Orthoptera. He used field observation, differential feeding tests, analysis of crop contents and fecal material, and the structure and adaptations of their mouth parts to foods to assess food preference for Michigan Orthoptera.

These studies and feeding observations have resulted in a more accurate determination of economically important rangeland species. Thus, figure 1 lists the species that might be considered of economic importance as consumers of forage plants on rangeland. This list is based on food preferences, distribution, abundance in past years of outbreaks, and abundance in more recent years. However, the species listed in figure 1 are not necessarily destructive every year, and species not listed in figure 1 may on occasion cause significant forage losses. Table 1 shows the preferred food plants of

COASTAL

Camnula pellucida (Scudder)
Cordillacris spp.
Dissosteira spurcata (Saussure)
Melanoplus devastator Scudder
Oedaleonotus enigma (Scudder)
Trimerotropis pallidipennis (Burmeister)

INTERMOUNTAIN

Ageneotettix deorum (Scudder)
Amphitornus coloradus (Thomas)
Aulocara elliotti Thomas
Boopedon nubilum (Say)
Camnula pellucida (Scudder)
Cordillacris spp.
Dissosteira spurcata (Saussure)
Drepanoptera femoratum (Scudder)
Encytoplophus sordidus costalis (Scudder)
Melanoplus foedus (Scudder)
Melanoplus sanguinipes (F.)
Oedaleonotus enigma (Scudder)
Trachyrhachis kiowa (Thomas)

GREAT PLAINS

Aeropedellus clavatus (Thomas)
Ageneotettix deorum (Scudder)
Amphitornus coloradus (Thomas)
Aulocara elliotti Thomas
Boopedon nubilum (Say)
Camnula pellucida (Scudder)
Chorthippus curtipennis (Harris)
Cordillacris spp.
Drepanoptera femoratum (Scudder)
Encytoplophus sordidus costalis (Scudder)
Eritettix simplex (Scudder)
Melanoplus infantilis Scudder
Melanoplus packardi Scudder
Melanoplus sanguinipes (F.)
Mermiria spp.
Morseiella flaviventris (Bruner)
Opeia obscura (Thomas)
Phibostroma quadrimaculatum (Thomas)
Phoetaliotes nebrascensis (Thomas)
Psoeoessa spp.
Trachyrhachis kiowa (Thomas)
Trimerotropis pallidipennis (Burmeister)

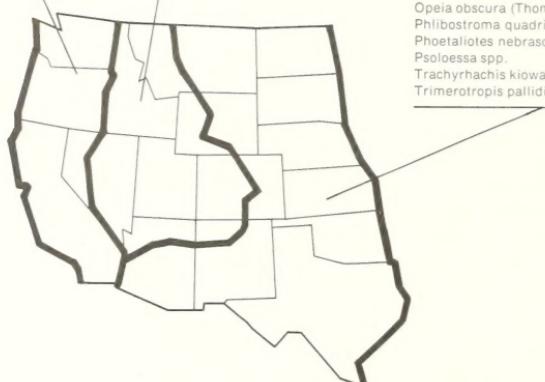


FIGURE 1.—Destructive grasshopper species of the Western United States shown according to geographical area in which they are most damaging. Their actual distribution may be much greater.

most of the important species as determined by some of the more comprehensive feeding studies.

Other workers have studied the preferred food plants of individual species. Pfadt (1949c) studied the importance of food plants in the ecology of *Melanoplus sanguinipes* in Wyoming, and Rogers (1974) gave a dietary analysis of this grasshopper within a cheatgrass community in Washington. Pfadt (1949a) also reported on the preferred food plants of *Aulocara elliotti* in Wyoming. The food preferences of *Dissosteira spurcata* in California were given by Kelly and Middlekauff (1961). Economic data on *Melanoplus devastator*, the most destructive grasshopper in California, were reported on by Harper (1952) and Middlekauff (1958).

Another variable that must be considered is the composition of grasshopper diets from hatching to

adults. Plant preferences expressed by adults may be different during nymphal development. These preferences may be due to different plants becoming available as the season progresses or other factors. A number of workers have studied this problem. In Kansas, both Lambley (1967) and Campbell (1967) found no significant changes in food plant preferences during the various stages of development of the species studied. However, Campbell mentioned that some species fed to a considerable degree upon *Bromus japonicus* Thunb. and *Poa pratensis* L. as first to third instars and seldom at all in later stages of their life cycle.

Alexander and Hilliard (1964) studied alpine populations of *Aeropedellus clavatus*. Their crop analysis indicated that the immature stages showed more variability in feeding than do adults, but all

stages showed a preference for grasses and sedges. Ueckert (1968) confirmed this species preference for grasses and sedges but concluded that preference for sedges decreased as the season progressed, whereas the preference for wheatgrasses and Idaho fescue, *Festuca idahoensis* Elmer, increased. Misra (1962), working with *Camnula pellucida* in the laboratory, concluded that the grasses best for survival and development changed weekly so that grasses which were best in the early stages of development may retard development in the later stages. He concluded a mixed diet would be most beneficial.

Gyllenberg (1969) studied food preferences for *Chorthippus parallelus* (Zett.) in Finland and concluded that the adults consumed mainly the same plant species as the nymphs, except for herbaceous plants that were only eaten by the nymphs. In the laboratory, the adults consumed grasses exclusively and the choice was widest during the third instar. Studies by Ueckert (1968) and Ueckert and Hansen (1971) showed that food preferences of a grasshopper species usually change seasonally, especially during the adult instar. This seasonal change in diet may be related to forage maturity and availability and to changing nutritional needs of the grasshopper. Allred (1941) reported that grasshoppers, mainly *Aulocara elliotti* and *Ageneotettix deorum*, which prefer grasses, killed 50 percent of a big sagebrush stand along the Little Powder River in Wyoming and Montana. On another occasion, *M. sanguinipes* fed readily on sagebrush over large areas in eastern Montana in 1939 even when moisture and grasses were available.

The demand on the food resource is spread out over an entire growing season, and a plant may be preferred by some grasshopper species during vegetative and succulent stages and by others during reproductive or wilted stages. Ueckert and Hansen (1971) found that plants are commonly more highly preferred when they are dried and wilted than when succulent.

Bernays et al. (1974) showed that the amounts eaten by *Locusta migratoria migratorioides* (R. & F.) on seedling grasses were less than on mature grasses. They found a higher grasshopper mortality with those grasshoppers that fed on the seedlings as compared with the mature grasses at all stages of nymphal development. Additional tests showed that an inhibitory substance in the seedling

leaves was probably acting as a feeding suppressant.

Grasshopper Density

Changes in grasshopper density throughout the summer must be considered when damage is related to the number of grasshoppers per square meter (Anderson 1972). Nakamura et al. (1971) discussed the population dynamics of a Japanese grasshopper population and concluded that *Parapleurus aliaceus* Germar decreased from 268 per square meter at the early nymphal stages in June to 68 adults per square meter in mid-August. Early instar mortality seems to be common with many species of grasshoppers, and parasites and predators also feed on later instars and adults. Hastings (1971) studied different populations of *Aulocara elliotti* to detect differences that could be correlated with grasshopper density; however, no direct relationship could be shown.

Kajak et al. (1968), in Poland, studied the effects of spiders on grasshopper populations by using cages covering 0.64 m². He concluded that, on the average, the presence of spiders reduced by about two times the losses in plant yield caused by the grasshoppers. Therefore, spiders may exert a significant influence on grasshopper populations and, thus, on the plant yield if grasshoppers and spiders are in the environment at the same time. However, as pointed out by Parker (1952), some species are early, others are intermediate, and some are late in hatching, reaching the adult stage, and ovipositing. Differences of 4 or 5 weeks have been found between early and late-developing species in Montana and Wyoming. Thus, grasshopper density is continually changing during the grasshopper season.

Habitat Preference

Vegetation definitely plays a role in determining grasshopper distribution and abundance beyond that of providing a source of food. A number of workers have described the preferred habitats of rangeland species. Clark (1947) found the optimal ovipositional habitat for the Australian plague locust to be areas lacking vegetation exceeding 15 centimeters in height with approximately 50 percent bare ground and 50 percent low cover. The optimal food shelter habitat of old nymphs and

adults contained a patchwork of tall and short cover, whereas young nymphs survived in high numbers on low vegetation providing green feed was plentiful. In general, he found that dense or tall vegetation is not readily warmed by the sun, nor so readily cooled by the free circulation of air as is thin vegetation. Consequently, dense vegetation is desirable for shelter, whereas thin vegetation provides better conditions for diurnal activity in favorable weather.

Anderson (1964) found grasshopper populations to be inversely proportional to the plant height and amount of shading. Plains areas were found to be occupied more frequently and in larger numbers when foliage cover was below 40 percent. In Arizona, Nerney (1960) found that as the length of the grass blades increased, perennial grass cover increased, total vegetation cover tended to increase, the grasshopper population decreased, and the percentage of damage to the perennial grass decidedly decreased. Dempster (1955), in Britain, investigating factors causing small-scale movement of *Chorthippus parallelus* and *C. brunneus* Thunb., found that nymphs and adult males tended to move from short into long vegetation, whereas females of *C. parallelus* showed a reverse tendency.

Bailey and Riegert (1971) thought that the food preferences of *Encoptolophus sordidus costalis* in Canada were related to the behavioral characteristics of the grasshoppers in their particular habitat. They observed this species to be a soil surface dwelling grasshopper. Since a preferred food plant such as *Carex eleocharis* Bailey is low growing, they suggest that the sedge is preferred because of the intimate association.

Ueckert et al. (1972) studied the influence of plant frequency upon the feeding habits and diets of 14 grasshopper species in Colorado. They found statistically significant correlations between the frequency of plants in the habitat and the frequency of plants in the grasshopper diets. They concluded that the diets of grasshoppers are influenced by the plant composition in the habitat, even though strong feeding preferences are expressed.

The diets of species that feed on a few plant species are generally influenced more by plant frequency than are diets of species that feed on many different plant species. According to some authors, the grouping or distribution of grasshoppers depends upon the type of soil. Isely (1938) noted that soil structure and texture play a part in grasshopper distribution and delimiting egg-laying sites.

Anderson (1966) indicated that *Aulocara elliotti* has a preference for undisturbed soil (as versus sifted soil) and found that egg pods were usually attached to solid objects such as small pebbles or roots.

Grazing Influence

A number of workers have recognized that depleted and overgrazed range is a favorite habitat for grasshoppers (Waldron 1898; Swenk 1913; Treherne and Buckell 1924; Ball 1936, 1937; Parker 1937, 1952; Dibble 1940; Mills 1941; Clark 1948; Nerney 1958; and Nerney and Hamilton 1969. Both Dibble (1940) and Parker (1952) stated that overgrazing by grasshoppers can be conducive to soil erosion, particularly when drought and mismanagement of the land also occur. Some quantitative results have been obtained regarding grazing pressure and grasshopper numbers.

In 1921, Buckell (1936) started an experiment to show the effect of overgrazing on the oviposition sites of *Camnula pellucida*. He fenced a 2-ha area that was normally used as an oviposition site by *C. pellucida*, and excluded all livestock. In 1921, when the grasshoppers returned to the egg beds for oviposition, they selected the closely grazed area outside of the fenced areas for oviposition. Buckell reported no eggs were laid in the 2-ha area for several years following the fencing. In Oklahoma, Coyner (1939) compared two overgrazed areas with a moderately grazed area. He collected 444 adult grasshoppers on the overgrazed areas and compared them with 63 on the moderately grazed area.

Weese (1939) also made a similar comparison except all orders of insects were included in his study. He found that the most abundant insects in the overgrazed area were the grasshoppers of the subfamily Cyrtacanthaeridinae. The total insect population in the overgrazed grassland is, on the average, approximately four times as great as in the normal prairie. An important factor in the distribution of grasshoppers and perhaps other insects is the presence of younger and more tender plants in the area in which the vegetation is kept down by the combination of livestock grazing and insect pressure. The relative number of insects collected by sweeping in the two types of habitat follows:

Order	Overgrazed area	Normal area
Coleoptera	23	10
Diptera	6	6
Hemiptera	12	2
Homoptera	43	10
Hymenoptera	28	6
Orthoptera	36	4

Smith (1940) also supported the findings of Weese (1939). He collected insects in Oklahoma in five pastures, which were grazed at different intensities. He found that the total number of insects increased under conditions of overgrazing, but the total number of species declined, except the Orthoptera, which was the only group to show an increase in both total number of species and total number of specimens. He reasoned that overgrazed pastures do not provide a favorable habitat for birds and small mammals that eat grasshoppers.

Nerney (1958) reported that in a heavily grazed sparse grass area about 70 percent of the herbage was eaten by an average of about 16.5 grasshoppers per square meter in comparison with about 20 percent by equal numbers in a moderately grazed fairly good perennial grass area. Batcheler (1967) studied populations of the grasshopper *Brachaspis collinus* Hutton in alpine meadows in New Zealand. He reported that populations of the grasshopper weigh less than 1.1 kg/ha in dense grassland and up to 32.2 kg/ha where scree forms a high proportion of the total cover. Biomass of grasshoppers was much greater than that of deer and chamois in the greater part of the alpine grassland above 1,524 m. Modification of the habitat because of grazing and trampling by the introduced ungulates is also believed to have favored grasshoppers, particularly in more dense grasslands.

More recently, Campbell et al. (1974) collected grasshoppers in Kansas from pastures grazed at different intensities and pastures moderately grazed on a 3-year rotational deferred grazing system. He found nymphs and adults more abundant in the heavily grazed pastures and least abundant in the deferred and lightly grazed pastures.

Human Influence

Forage consumption by grasshoppers probably has been influenced greatly by man's activities on rangeland. Ball (1936) stated that all ranges are overgrazed; however, this condition is no longer as widespread as during the early cattle days. Treherne and Buckell (1924) believed that early overgrazing by livestock was primarily responsible for the disappearance of the range grasses from Canada and that drought and the influence of grasshoppers are secondary factors.

Parker (1940) viewed the present land-use system in the Western States as more favorable for grasshoppers than during the early development of western agriculture. He stated that roadsides,

fence rows, ditchbanks, grain stubble, idle land, untilled crops, and depleted ranges all provide more favorable egg-laying grounds than the original grasslands and that a more abundant supply of green food is provided for a longer period each summer by the growing of agriculture crops.

Riegert et al. (1965), from observing large populations of *Cannula pellucida* in Canada, stated that severe infestations were usually associated with and dependent upon nearby cultivated crops. The native grasslands, in general, possess the necessary attribute of an oviposition habitat but do not provide the suitable food habitat for this species except for mountain meadows or native grass foot-hill areas.

Bei-Bienko (1930) reported on plant association changes in Russia that because of grazing, woodcutting, and farming practices, resulted in a more favorable habitat for certain grasshopper species. He said grasshoppers migrate to the newly formed plant associations, and some species cause serious damage to cultivated crops in these areas.

More recently, Hewitt and Rees (1974) found that certain land renovation practices, such as furrowing and scalping used in the Western United States, can provide an unfavorable habitat for some species of grasshoppers. Scoggan and Brusven (1973) also studied the grasshopper-plant community associations in Idaho in relation to the natural and altered environment. Habitat alterations such as fire, soil tillage, sagebrush treatment, logging, road construction, and overgrazing all affected grasshopper distribution and abundance. Campbell et al. (1974) collected grasshoppers in Kansas in pastures that had been burned in early spring, midspring, and late spring. Both nymphs and adults were most abundant in the areas burned early in the spring.

Weather Influence

Attempts to make a direct correlation between the fluctuation of grasshopper numbers and weather, especially on a short-term basis, have mostly been unsuccessful. However, Nakamura et al. (1975) reported that adverse weather conditions during egg development and first instar development caused variation in grasshopper numbers during the sampling period. In general, the more warm or hot days in a summer the more time available for grasshopper feeding. As Parker (1954) pointed out, grasshoppers eat more in hot weather than in cool weather.

Pepper and Hastings (1952) determined that

under field conditions, the greater portion of the energy that results in raising the body temperature of grasshoppers comes from the absorption of direct solar radiation. Some species differ in their ability to absorb radiant energy, and, thus, grasshopper feeding may be affected by such differences. These authors also report that grasshoppers climb on vegetation to orientate themselves to the sun's rays during cool weather, such as in the fall, and may remain in that position throughout the day. This may result in reduced feeding.

In New Zealand, White (1974a) measured the incidence of adult grasshopper activity relative to the level of insolation and determined that a decline of activity begins when insolation approaches $2.0 \text{ cal cm}^{-2} \text{ min}^{-1}$. He also monitored the temperature, or the temperature at which grasshoppers become active in the base of plants, and found that the threshold temperature approximates 3° to 4° C . However, weather indirectly affects grasshoppers through its direct effect on vegetation.

Nerney (1960, 1961) and Nerney and Hamilton (1969) reported that on poor or overgrazed range-land, grasshopper populations are greater after years with normal or above-normal precipitation than after those with unusually light precipitation. Apparently, average or above-average precipitation allows more plant species to become available for grasshopper feeding. In Arizona, spring-hatching species are of greater economic importance, and outbreaks occur more frequently than with the summer-hatching species. Thus, early rainfall is important to the development of grasshopper populations in Arizona. This situation is different from that in the Great Plains where overgrazing, erosion, and drought are usually associated with grasshopper buildups. In this area, during times of cool weather and abundant rainfall, grass is likely to be plentiful, and the amount consumed by grasshoppers may not be economically significant. In hot dry weather, however, grass is likely to be scarce, and the amount consumed by grasshoppers may be very important. Certainly, the weather pattern in any one area may favor certain plants and tend to decrease or eliminate others. Perhaps as a result of these vegetational changes, food and shelter conditions might be produced that would be either more or less favorable to different grasshopper species. Some authors have also reported that early warm weather followed by cold weather can cause a high

grasshopper mortality (Shotwell 1929; Parker 1928).

Physiological Influence

Only general statements can be made regarding the amount of food consumed by grasshoppers during their development. Langford (1930) pointed out the wide variation in the amount of food eaten by individuals of the same brood hatched from the same egg pod and reared under the same conditions.

Anderson (1970) stated that whether a population is vigorous and increasing in numbers or lethargic and decreasing may have an effect upon the amount of vegetation destroyed. He felt that when a population grows individuals spend less time fighting among themselves and more time feeding. Conversely, a population that has reached peak numbers or is decreasing seems to be more excitable and spends less time feeding. Generally, food consumption in Orthoptera increases in direct proportion to size during nymphal stages (Gangwere 1959). Langford (1930) remarked that with each molt a grasshopper almost doubles the amount of food eaten daily. His laboratory tests with *Melanoplus differentialis* (Thomas), *M. bivittatus* (Say) and *M. femur-rubrum* showed that adult females eat almost 100 times more food per day than first instar nymphs.

Smith (1959) studied *Melanoplus sanguinipes* in the laboratory and found no difference in the amount of food consumed and utilized between the sexes. Langford (1930), on comparing 113 males with 94 females, found that the females ate from 1.8 to 3.6 or an average of 2.5 times more food than males in a 12-hour day. The female ate from 8.0 to 260.5 percent more food per day than the males. Matsumoto (1971) conducted laboratory feeding tests in Japan and also found that females ate more than males.

Gangwere (1959) explained that while females of a species eat more than males, they eat less per unit of weight, as would be expected from their lesser activity and lower metabolic rate. He says the consumption ratio between male and female is relatively constant even under fluctuating environmental conditions, for changes in temperature and humidity alter gross consumption without affecting the ratio.

ESTIMATES OF FORAGE LOSSES

Estimates of the amount of forage loss due to grasshoppers have been reported in dollars, in acres infested, in cost of control, in percentage of vegetation destroyed, and as forage consumption compared to livestock. Most estimates of monetary forage losses are given for the 1930's because numerous grasshopper outbreaks occurred during those years.

Morton (1939) estimated from Forest Service figures that during 1934 grasshopper damage to rangeland in Colorado, Montana, Nebraska, North Dakota, South Dakota, and Wyoming amounted to \$2,455,000. This figure represented only the value of the forage destroyed and did not include indirect losses by importation of feed, removal of livestock, forced sale of livestock on low markets, liquidation of foundation stock, and increased erosion due to reduced vegetation cover. He also estimated that during 1935 and 1936 losses were probably just as great.

Pfadt (1949b) reported that C. L. Corkins, State entomologist of Wyoming, aided by the county agents estimated that the loss in Wyoming in 1936 due to range grasshoppers amounted to \$1,480,000. Hinkle (1938) reported that one species of grasshopper, *Dissosteira longipennis* (Thomas), caused \$1,500,000 damage to crops and forage in Colorado in 1937. A summary of losses from 1925 to 1934 was reported for Canada by Buckell (1936) and for the United States by Parker (1937). Knowlton (1952) estimated damage in Utah at \$200,000 per year since about 1934 after organized control programs were established. Parker and Connin (1964) stated that the average yearly loss to range and pasture grasses is estimated to be about \$80 million in 17 Western States.

Figures given for controlling grasshoppers or hectares infested usually included mixtures of both cropland and rangeland. For example, Knowlton (1966) reported that 194,800 ha of range and cropland were infested in Utah in 1966. Parker (1933) reported a grasshopper outbreak in South Dakota, North Dakota, Nebraska, and Iowa in 1931 which included 43,518 km² of which 19,199 km² were in crops. McDonald (1965) reported that in 1962 about 23,200,000 hectares of land were infested in Manitoba, Saskatchewan, and Alberta. Following con-

trol by baits and insecticides, a number of workers reported on the value of such control campaigns.

Parker (1933) reported on a 10-year period, 1913-23, in which eight States and three Provinces were treated. A total of \$3,265,189 was spent on grasshopper control with an estimated savings of \$141,692,975. He also reported the largest expenditures recorded as being \$604,571 for North Dakota in 1919 and \$540,000 for Alberta in 1922. Paul (1940) estimated crop damage (probably wheat) from Saskatchewan in 1934 based on farm records. He said crops valued at \$605.61 per farm were saved as a direct result of grasshopper control. The average crop loss was 24 percent, whereas without control the damage would have been almost three times as great, 66 percent. An average gross savings of \$5.23/ha was obtained from a total bait cost of \$0.16/ha.

Munro (1949) stated that the total cost of grasshopper control was \$27,337,808 in 24 States during 1936-47. He conservatively estimated that these expenditures resulted in savings of \$693,323,388 worth of crops during the 12-year period. McDonald (1965), using the calculations of W. B. Fox, estimated the value of the crop saved per dollar expended for grasshopper control in Alberta to range from \$100 to \$200 for 1949-53. Harper (1952) gave the figures for the 1952 season in California as 116,000 ha treated at an approximate expense of \$610,000 and a crop savings of \$13 million.

A number of workers have also estimated the amount of forage consumed by different grasshopper densities but have failed to consider the food preferences of the various rangeland species. Drake and Decker (1932) stated that as a grasshopper generally eats about one-tenth of its weight at a meal and as it frequently feeds several times a day, an individual may consume about one-half its weight of green food every 24 hours. They also reported that when grasshoppers in a field average about 20.4 per square meter they will consume approximately 900 kg of alfalfa hay per day.

Cowan (1958) estimated that grasshoppers annually consume from 6 to 12 percent of the available forage in the Western States. This amounts to between 4,205,700 and 8,984,700 metric tons (t), which would support from 2,492,000 to 5,324,000 additional animal units. Forage utilization by grass-

hoppers has also been compared to utilization by livestock. Drake and Decker (1937) estimated that 12 to 24 grasshoppers (depending upon size) per square meter in a 0.4-ha area of bluegrass pasture will consume as much forage daily as a cow. Parker and Connin (1964) mentioned that even with an average of seven or eight grasshoppers per square meter the population on 4 ha consumes grass at about the same rate as a cow.

During outbreaks when there may be 36 to 72 grasshoppers per square meter, all the grass may be destroyed. Nerney and Hamilton (1969) reported that in 1954 in Arizona 99 percent of the vegetation was destroyed by *Aulocara elliotti* at a density of 50 to 77 grasshoppers per square meter. Nerney (1960) also found the total damage caused by 11 to 32 grasshoppers per square meter to range from 8 to 63 percent.

QUANTITATIVE STUDIES ON FORAGE LOSSES IN AREAS OTHER THAN THE WESTERN UNITED STATES

Several workers have attempted to quantitatively measure forage losses caused by grasshoppers in the laboratory and in the field. A few workers have found that grasshoppers have a minimum influence on vegetation; however, these studies have involved grasshoppers that are not associated with U.S. rangeland. For instance, Matsumoto (1971) in Japan determined that a field population of *Parapleurus aliaceus* consumed 242 g dry wt of *Miscanthus sinensis* Anders leaves per 100 m² in 1968 (1.4 percent of the standing crop in August) and 97.6 g dry wt/100 m² in 1969 (0.6 percent of the standing crop in August). He also added that even if the indirect effects of feeding are considered, the loss of the primary productivity of *M. sinensis* grassland due to *P. aliaceus* would rarely exceed 5 percent.

Other workers have determined the amounts of forage consumed and assimilated in terms of energy units. Smalley (1960) reported on a marsh grasshopper population (*Orchelimum fidicinium* Rehn and Hebard) in Georgia and found that less than 1 percent of the dominant plant (*Spartina alterniflora* Loisel) was eaten by the grasshoppers. He concluded that most of the net primary production of the marsh is eventually decomposed. Wiegert (1965) studied populations of grasshoppers on two sites in Michigan, an old field and an alfalfa field. On the old field, the grasshoppers ingested 4.8 kcal/m²/year (less than 0.5 percent of the net primary production), while the ingestion by grasshoppers on the alfalfa field was 36 kcal/m²/year (approximately 2.5 percent of the net primary production). Populations at both sites in general ranged from 10 to 11 individuals per square meter in early summer to less than one per square meter in September and October.

Based on studies in Finland with *Chorthippus parallelus*, Gyllenberg (1969) mentioned that when consumption versus net primary production is considered in the course of time, the part eaten at first constitutes a very small percentage of the material produced by the plants, but as plant production decreases, grasshoppers comprise a regulating factor on the new plant biomass produced. However, he also concluded that the grasshopper population was not a factor regulating the amount of net primary production.

White (1974b) estimated consumption of field populations of alpine grasshoppers by using field data such as consumption per grasshopper per feed, feeding thresholds, the number of feeds in a lifespan, grasshopper density, feeding preference, and vegetation availability. He estimated that instars 4, 5, and 6 and adults of *Paprides nitidus* Hutton accounted for more than 90 percent of the cumulative consumption in the total lifespan of the individual. In areas of high grazing pressure, the amount of vegetation removed was only 13 kg/ha where the total dry matter productivity was estimated to be 500 to 600 kg/ha. However, the authors pointed out that the selective distribution of grazing activity may contribute to pressure in excess of 50 percent on some vegetation components.

White (1974c) surveyed 10 alpine sites in New Zealand and compared grasshopper density, consumption level, vegetation composition, percent bare ground, and site aspect. He concluded that in most tussock grasslands below 1,200 m, grasshopper grazing pressures are negligible because of low grasshopper densities and noncritical levels of vegetation productivity, but in grasslands above 1,200 m, grazing pressures are of real significance because densities are high and crop availability and

production are low. However, most studies have shown that grasshoppers and locusts cause considerable forage losses.

The most difficult task is to compare results of the different research efforts on an equal basis. For example, Andrzejewska et al. (1967), in Poland, calculated that 10 acridoidea per square meter reduced the net primary production 11.9 percent during a 9-week period and estimated that grasshoppers destroy nearly five times the biomass they consume.

Rubtsov (1932) concluded that 10 grasshoppers per square meter in eastern Siberia would consume 683 kg/ha of grass for a total loss in that area of 38,970 t/year. This was based on feeding studies that showed that an adult eats 30 to 50 percent of its own weight in grass (*Bromus inermis* Leyss) each day, and, during its development, an adult individual consumes 20 times its weight. Serkova (1961) reported that, in Russia, a grasshopper population of one to two per square meter in 1958 destroyed 15.6 percent of the vegetation during the growing season, whereas in 1955 a population two to three times greater destroyed 30 percent of the vegetation.

Researchers outside of the United States have studied forage losses caused by individual grasshopper species. Davey (1954) working with the desert locust, *Schistocerca gregaria* (Forsk.), figured that males consumed an average of 30.7 g of fresh vegetation and females 44.3 g between hatching and becoming adults. He also determined that a nymph eats approximately its own weight of fresh vegetation per day, and an adult roughly one-half its own weight per day (approximately 1.0 g). A migrating swarm would need to eat at least its own weight per day and possibly three times as much. Bullen (1966) using these data suggested that a fairly typical desert locust swarm (26 m² in area), with an area density of 36 locusts per square meter and a mean weight per locust of 1.7 g, could consume at least 1,413 t of fresh vegetation per day. The amount damaged, destroyed, and left uneaten

should also be considered. He related forage losses to grazing by considering that the optimum carrying capacity in African semiarid desert areas is often one cow to 16 to 20 ha and can be as low as one cow to 26 ha in the semidesert areas of the Sudan. From the known food consumption of the desert locust, Bullen estimated that a swarm of 240 per square meter could eat as much vegetation per day as one native cow (about 11 kg), so that a small to medium swarm of about 26 km² has the grazing capacity of 150,000 head of cattle, or about 1,000 times the ecological optimum carrying capacity of the growing area.

Kaufmann (1965) determined the food consumption of *Euthystira brachyptera* (Ocskay) in central Europe by offering caged grasshoppers preferred and unpreferred food plants. He found six third instar nymphs consumed an average of 1.897 g of preferred fresh vegetation and 1.736 g of unpreferred fresh vegetation during a 2-week period when the temperature ranged from 20° to 27° C. He also found the average daily consumption of fresh vegetation by adults at different temperatures to be as follows:

Temperature °C	Fresh vegetation consumed (mg)	
	Male	Female
16	17	28
18	26	34
20	23	43
22	23	51
24	24	61
26	36	68
28	38	84
30	42	98

More recently, White and Watson (1972) studied food consumption of three New Zealand alpine grasshoppers by counting leaves and measuring the amount of leaf area destroyed. They determined the dry weight consumption for each instar of the three species and the number of feeds that occur within each instar. The number of feeds (generally two per day) is limited by the level of incoming radiation that is sustained during the day.

FORAGE LOSSES CAUSED BY GRASSHOPPER POPULATIONS IN THE UNITED STATES

Workers in the United States and Canada have assessed forage losses caused by grasshoppers both in terms of populations and as individual species. Morton (1936) was one of the early workers to

determine forage losses caused by a mixed population of rangeland grasshoppers. He selected 10 stations in various types of range in Montana and placed two cages (1 m²) on each site to exclude all

grasshoppers. He clipped two quadrats at intervals of from 1 to 2 weeks at each station until August 14th at which time the cages were removed, vegetation inside was clipped, and the number of grasshoppers per square meter was calculated. He determined that the amount of dried vegetation destroyed averaged 41.0 g/m² and the average number of grasshoppers in early June was 22.7 per square meter, indicating that each grasshopper at that time destroyed 1.806 g of vegetation in 2 months. However, the actual amount consumed was 13.43 g/m², only one-third of the total vegetation destroyed. The effect of screening on the vegetation was not measured. The author further calculated that a 450-kg cow would require a minimum feeding requirement of 9 kg/day of dry range grass or 272,160 g/month. On the basis of 1.806 g of vegetation being destroyed by one grasshopper in 2 months (0.903 g/month), a population of 74 grasshoppers per square meter over 1 hectare would destroy vegetation at the same rate as 2.5 cows per hectare.

With lighter stands of vegetation requiring more hectares per cow, smaller numbers of grasshoppers per square meter would cause equivalent damage. Morton (1939) continued the above study, but in this later work one cage contained no grasshoppers and the other cage was infested with the same number as were present per square meter on the outside. This was changed to determine the effect of grasshopper cages on vegetation. He determined that, in Montana, cages increased grass growth 5.5 percent and forb growth 77.5 percent, whereas grasshopper damage amounted to 44.3 percent to grass and 48.2 percent to forbs. The average number of grasshoppers maintained in the cage was 18.6, which varied from a high of 29 in June to 3 in September. In Wyoming, cages increased grass growth 13.9 percent and forb growth 41.4 percent, whereas grasshopper damage amounted to 59.2 percent to grass and 46.5 percent to forbs. The average number of grasshoppers maintained in the cage was 14.4, which varied from a high of 26 in June to 2 in September. In 1938, favorable growing conditions existed at both locations, grasshopper populations were low and forage was undamaged.

Hinkle (1938) also studied forage utilization by grasshoppers in Colorado with the use of cages. He determined that the greatest utilization occurred between August 8 and August 28; more than 50 percent of buffalograss, *Buchloe dactyloides* Nutt.

Engelm., western wheatgrass, and bluegrama were destroyed by native species. The period of peak grass production occurred during the time of greatest utilization.

Pepper et al. (1951) also reported on grasshopper populations in two plant communities (western wheatgrass and needleandthread-western wheatgrass) in Montana. Part of each community was sprayed to control grasshoppers, and quadrats (122 by 122 cm) were clipped in both sprayed and unsprayed areas. Areas were clipped on July 6 to 14 right after spraying and twice at monthly intervals for a total of 87 quadrats in the sprayed area and 114 in the unsprayed area. Grasshopper populations were measured by the cage method every third day. The following data were taken:

Weight of grass clippings (period of test 2 months)
(Expressed in kilograms per hectare air-dry weight)

	Grass-hoppers per square meter	1st clip	2d clip	3d clip	Increase or decrease
<i>Sprayed Area:</i>					
Wheatgrass type	<1	497	613	689	+ 192
Needlegrass— wheatgrass type	<1	743	900	783	+ 40
<i>Unsprayed area:</i>					
Wheatgrass type	8	586	370	303	- 283
Needlegrass— wheatgrass type	9	635	581	356	- 279

Total utilization by grasshoppers is the sum of the loss in weight on the unsprayed area plus the gain in weight on the sprayed area. This would amount to 469 kg/ha on the wheatgrass type and 316 kg/ha on the needlegrass-wheatgrass type or an average of 369 kg/ha. If one were to assume that in the absence of grasshopper utilization this range would yield the weight of grass present on the date of the third clipping on the sprayed area, the amount of grass consumed by grasshoppers would amount to 55 percent of the total yield. The authors concluded that if grasshoppers were eliminated, grazing capacity would be increased by approximately 50 percent.

Anderson and Wright (1952) also compared net primary production on sprayed and unsprayed ranges in Montana by clipping vegetation. They found at one location that 52 percent of a dense stand of *Agropyron smithii* (western wheatgrass)

was removed by an average population of 9.25 grasshoppers per square meter and 62 percent of a sparse stand was damaged by an average population of 4.19 grasshoppers per square meter. They concluded that heavy damage could result from a comparatively low population, and that little relationship exists between the amount of damage and number of grasshoppers per square meter unless the species are known. Western wheatgrass was particularly susceptible to damage by four species: *Drepanoptera femoratum*, *Metator pardalinus* (Saussure), *Aulocara elliotti*, and *Phoetaiolites nebrascensis*.

In another study, Anderson (1961) found little correlation between numbers of grasshoppers per unit area and the loss of vegetation. He accounted for this by the differences in feeding habits of the various species comprising the particular grasshopper population. He also stated that considerable reductions of yield of vegetation could take place during a season without any grazing by either livestock or grasshoppers.

Nerney (1966) recorded the amounts of forage eaten or cut off by grasshoppers in Arizona on both sprayed and unsprayed areas. He recorded the amount of damage to each plant species contacted by a point frame technique. Nerney considered damage measurements up to 20 percent, light; from 20 to 35 percent, moderate; and from 35 to 40 percent, heavy. He reported that in 1964 *Melanoplus*

sanguinipes consumed 92.5 percent of the available herbage, mostly *Sitanion hystrix* (Nutt.) J. G. Smith (bottlebrush squirreltail).

In 1965, the percentage consumed was low as grasshopper populations were noneconomic. Nerney and Hamilton (1966) utilized the same approach and reported that from August 4 through September 8 the amount of grass destroyed by average grasshopper populations of 54 per square meter, mostly *Morseiella flaviventris* (Bruner), was about 675 kg dry wt/ha. Nerney and Hamilton (1967) reported that by September 7th of that year percentages of grass consumed by one grasshopper per square meter in the untreated area were 2.72 percent for blue grama, 1.41 percent for curly mesquite [*Hilaria belangeria* (Steud.) Nash], 3.38 percent for three awn (*Aristida* spp.), 7.68 percent for sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), and 2.80 percent for watergrass. A survey in October showed the amount of three awn, Lehman lovegrass (*Eragrostis lehmanniana* Nees), and sideoats grama blades utilized by grasshoppers as heavy (35 to 50 percent). The flowering seed heads of sideoats grama and Lehman lovegrass were most preferred as food, and the seed crops of these plants were 90 to 95 percent destroyed by a population averaging 33 per square meter with *Morseiella flaviventris* comprising 74 percent of the total population.

FORAGE LOSSES CAUSED BY INDIVIDUAL GRASSHOPPER SPECIES IN THE UNITED STATES

A number of workers have studied the food consumption and forage losses caused by individual grasshopper species. At least three workers have been concerned with alfalfa destruction by grasshoppers (Morrill 1918; Langford 1930; and York and Prescott 1947). However, the most significant studies regarding rangeland losses have been conducted with grasshopper species found to be economically important on rangeland since the last major outbreaks of the 1930's. Pfadt (1949b) used cages on Wyoming rangeland to determine forage reductions per hectare caused by different densities of *Aulocara elliotti* as follows:

Nymphs per square meter	Kilograms of forage reduction per hectare
18	457
30	550
42	891

Because forage production on the study site was 1,350 kg/ha, a population of 18 grasshoppers per square meter would reduce the forage approximately 66 percent assuming 50 percent of available forage is normally utilized by livestock.

Putnam (1962) in Canada also used cages over natural sod and recorded the reduction in yield by the different instars of *Camnula pellucida* and *Amphitnorus coloradus* as follows:

*Forage reduction (kilograms per hectare)
at 1 grasshopper per square meter*

Instar	<i>Camnula</i> <i>pellucida</i> feeding on <i>Poa pratensis</i>	<i>Amphitornus</i> <i>coloradus</i> feeding on <i>Stipa comata</i>
1953, 1st-5th incl.	5.85	
1954:		
1st	.118	--
2d	.362	0.375
3d	.853	.629
4th	2.216	1.733
5th	5.715	3.926
Adult	11.475	7.110

Thus, during the nymphal life of *C. pellucida*, the yield was reduced by 5.8 kg/ha for each grasshopper per square meter and 3.9 kg/ha for *A. coloradus*. Putnam stated that young *C. pellucida* adults reduced the yield by about 95 mg per grasshopper per day and destroyed as much in 5 days as in their whole period of nymphal growth. Each young adult of *A. coloradus* reduced the yield by about 53 mg per day. He concluded that 24 adults per square meter of either species could take the entire available yield if 50 percent of the available forage can be safely harvested. Putnam (1962) suggested that the appropriate stage at which to control such a population would be the third instar, on the assumption that recruitment by this time is negligible and that the maximum rate of damage occurs during the adult stage.

Randell (1970), who developed a model based on Putnam's findings with *C. pellucida*, suggested that the timing of control measures may be more critical because according to his model the maximum rate of damage occurs when the population is in the fourth instar when numbers and appetite combine to yield the highest feeding rate. His model also suggested that the greater numbers of young nymphs contributed more than $\frac{1}{4}$ of the total damage as opposed to $\frac{1}{6}$ to $\frac{1}{7}$ suggested by Putnam. Randell (1970) also determined for *Melanoplus sanguinipes* a value of 356 mg as the dry weight of food required per individual from hatching to the adult stage. When used in this model, this figure suggested that a total consumption of 394 kg/ha (dry wt) is a valid estimate of the total consumption of a population of 24 grasshoppers per square meter at the adult stage experiencing normal field mortality.

Misra and Putnam (1966) carried out laboratory

and field experiments with *Camnula pellucida* to compare food consumption between laboratory and field reared grasshoppers. They determined the dry weight of *Poa pratensis* required to rear grasshoppers from hatching to the adult stage as 321 mg per insect in the laboratory and 476 mg per insect in the field. This is equivalent to a consumption of 3.8 and 5.7 kg of forage per hectare by an infestation of one grasshopper per square meter during the nymphal life. A loss of 38.7 mg per day was determined for each adult reared in the laboratory and 96.1 mg per day for those reared in the field.

Pruess (1970) compared ingestion of bluestem and ragweed between populations of adult *Ageneotettix deorum* from Nebraska and Kansas. He found that in 6 days of feeding the Nebraska grasshoppers ingested 81.4 mg per grasshopper and the Kansas grasshoppers, 85.1 mg per grasshopper. He concluded that plants from Kansas were more digestible for both grasshopper populations; however, ragweed from neither source was acceptable nor utilized by either grasshopper population.

Parker (1930) was probably the first worker to determine food consumption for *Melanoplus sanguinipes*. He fed wandering-Jew (*Zebrina spp.*) to nymphs held at different temperatures in the laboratory with the following results:

Food consumption (mg) by 10 nymphs (during nymphal stage) at constant and alternating temperatures

Temperature (°C)	Constant temperature	Alternating ¹ temperature
27	6,796	4,700
32	6,959	5,061
37	7,179	4,639

¹ 16 hr at 12° C and 8 hr at 27°, 32°, or 37° C.

Parker concluded that there was a 24-percent reduction in food consumed and a 30-percent reduction in the time spent in the nymphal stage by those grasshoppers reared under alternating temperatures. The author also found that 10 adults during a period of 20 days consumed 11,587 mg at 37° C, 8,929 mg at 32°, and 4,836 mg at 27°. He stated that, generally, immediately after the adult stage is reached, daily food consumption increased rapidly and reached its maximum in about a week, at which time it may be from 50 to 75 percent greater than during the last nymphal instar. From 21° to 27° C, feeding activity is greatest and will decrease rapidly at both above and below these temperatures. Grasshopper damage should, therefore, be

more severe during periods of high temperatures because of the greater amounts of food consumed. Parker (1952) also reported that on the basis of outdoor cage experiments an adult grasshopper of the larger rangeland species consumes 30 mg of vegetation (dry weight) per day, and because one *M. sanguinipes* consumes 24 mg/day at 27° C as reported above, then 74 larger grasshoppers per square meter would consume forage equivalent to that of a cow.

Smith (1959) also reported on food consumption, utilization, and weight gain of adult *Melanoplus sanguinipes* for 5-day periods on three food plants as follows:

Food plant	Totals for 8, 5-day periods	
	(40 days)	Mg dry weight
Food consumed:		
Wheat	714.9	
Western wheatgrass	810.1	
Oats	373.0	

Food plant—Continued	Totals for 8, 5-day periods	
	(40 days)	Mg dry weight
Food utilized:		
Wheat	231.7	
Western wheatgrass	259.7	
Oats	119.0	
Gain in weight:		
Wheat	70.2	
Western wheatgrass	68.9	
Oats	43.4	

The utilization of oats differed significantly from the other two food plants in all three tests.

Appendix table 2 contains a summary of forage losses from U.S. studies based on field populations and the amount destroyed by species during nymphal and the adult stages combined. Appendix table 3 contains forage losses determined separately for nymphs and adults of individual species and/or in the laboratory and field.

SUMMARY AND RECOMMENDATIONS

Grasshoppers have been and still are the major invertebrate pest on millions of hectares of rangeland in the Western United States, and much time and effort have been given to the research of this group. However, little real progress has been made to determine the actual amount of forage lost under the different grazing situations, and the information available is seldom utilized in control decisions. In the United States, grasshoppers are controlled by individual land managers, private organizations, and by State and Federal Government agencies. Expensive and intensive grasshopper control measures are based largely upon the number of individuals per unit area. Species composition, rangeland vegetation, watershed management, and grazing systems are usually ignored when control recommendations are made.

The role of grasshoppers as grazing animals in competition for forage with livestock and wildlife needs additional study and one of the basic criterion for evaluating this role is the determination of forage losses resulting from a particular grasshopper population. However, unstable weather patterns, fluctuating grasshopper numbers, and a changing vegetational complex make predictions regarding forage losses with our present knowledge very unreliable or impossible. Therefore, an approach is suggested as reported on by White and Watson

(1972), and White (1974a, 1974b, and 1974c), in New Zealand, mainly using field data.

Grasshopper populations in the major rangeland types (northern shortgrass rangeland, southern plains area, intermountain region, and coastal area) need to be studied in detail in association with the vegetation and weather patterns of the area. The following information is needed on grasshopper populations from the time of hatching until grasshopper abundance decreases to near zero: (1) Density, (2) length of each instar, (3) number of feeds per day or number of minutes spent in feeding each day, (4) amount of forage (mg) consumed or destroyed per feed or during a certain period of activity (time temperature is >21.1° C), and (5) grasshopper mortality resulting from parasites and adverse weather conditions. (Predation by birds, mammals, and insects is less variable since most of these predators are territorial by nature, and, thus, their numbers are fairly constant from year to year unless major vegetational changes take place.)

The above information should be recorded for each instar of the more abundant grasshopper species present. In addition, weather data such as ground surface temperature, soil temperature and moisture, and precipitation need to be correlated with grasshopper and plant development, especially to predict forage production on the various

rangeland types. Weather records can also be used to determine the average hours available for feeding during any summer day and for establishing similar conditions in the laboratory for feeding trials. This approach assumes that food preferences for the more important species are known.

The objective of this study is to be able to derive a prediction equation to calculate forage losses with

acceptable accuracy once key items concerning the population and environment are known. However, additional testing at various sites within a rangeland type would be necessary to validate this approach. I hope that this plan of study will aid research workers, assist control personnel in evaluating grasshopper infestations, and, eventually, result in better management of our rangeland areas.

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APPENDIX TABLES

TABLE 1.—Preferred food plants of destructive rangeland grasshopper species as reported by specific researchers

		Grasshopper preferred food plants ¹						
Economic grasshopper species		Alberta, Saskatchewan, and Manitoba	Montana	Nebraska, North Dakota	Colorado	Idaho	Idaho Banfill and Brusven (1973)	Kansas Campbell et al. (1974)
<i>Aeropedellus clavatus</i>	25			20,17	20	10,23,14	2,13	5,22,33
<i>Ageneotettix deorum</i>	4		23,10, 4	20,10,22	10,20	10,23	6	10,20,11
<i>Amphibotrus coloradensis</i>	23			20,10,23	10,23		6,13	
<i>Aulocara elutatu</i>	4				10,23			
<i>Boopedon nubilum</i>								
<i>Cannula pelicina</i>								
<i>Chortophaga curtipennis</i>								
<i>Cordillacris</i> spp.	10,25		4,23	28,18,24	3,16	8,20	20,29	12,21,15
<i>Dissosteira spicata</i>				20				15,23,26
<i>Drepanoptera femoratum</i>				14,27,22	10,23	10,23, 4	6,13	
<i>Enoplophilus sordidus</i>								
<i>costalis</i>	4		4	20,10	20,10	14,10,23		
<i>Eritettix simplex</i>			10	10,14,20	10			
<i>Melanoplus devastator</i>								
<i>M. femur-rubrum</i>								
<i>M. infantilis</i>	4,25			30,31,43	30,31,43	30,34	13	13,32,36
<i>M. packardii</i>	39				10			
<i>M. sanguinipes</i>	4,41,42			30,31,43				30,31
<i>Mermiria</i> spp.	9,14	9,14		20,31	20,10		33	20,43,30
<i>Morsella flaviventris</i>								
<i>Oedaleonotus enigma</i>								
<i>Opelia obscura</i>	10	4	10		10			10
<i>Phihistruina</i>								
<i>quadrimaculatum</i>	10				10			
<i>Phoebaliotes nebrascensis</i>	4			20, 8	4, 8,20		1	
<i>Pseudeesa</i> spp.								
<i>Trachyrhachis kowa</i>	10,4		23, 4,37	10, 3,20	10	10	6	
<i>Trimetropis pallidipennis</i>								5,19,38

¹ The first plant listed is the most preferred.² Numbers in columns correspond to the following list:

GRASSES:

1. *Agropyron dasystachyum* (Hook.) Scribn.
2. *A. desertorum* (Fisch.) Schult.
3. *A. repens* (L.) Beauv.
4. *A. smithii* Rydb.
5. *A. spicatum* (Pursh) Scribn. & Smith
6. *A. species*
7. *Andropogon gerardii* Vitman
8. *A. scoparius* Michx.
9. *Bouteloua curtipendula* (Michx.) Torr.
10. *B. gracilis* (H.B.K.) Lag. x Steud.
11. *B. hirsuta* Lag.
12. *Bromus inermis* Leyss.
13. *B. tectorum* L.
14. *Calamovilfa longifolia* (Hook.) Scribn.
15. *Festuca idahoensis* Emer
16. *Hordeum jubatum* L.
17. *Koeleria cristata* (L.) Pers.
18. *K. species*
19. *Phleum pratense* L.
20. *Poa sandbergii* Vasey
21. *P. species*
22. *Sporobolus cryptandrus* (Torr.) A. Gray
23. *Stipa comata* Trin. & Rupr.
24. *S. species*
25. *Carex filifolia* Nutt.
26. *C. geyeri* Boott
27. *C. pensylvanica* Lam.
28. *C. species*
29. *Achillea millefolium* L.
30. *Ambrosia psilostachya* DC.
31. *Amorpha canescens* Pursh.
32. *Chrysopsis villosa* (Pursh.) Nutt.
33. *Erodium cicutarium* (L.) L'Her.
34. *Evolvulus nuttallianus* R. & S.
35. *Medicago lupulina* L.
36. *M. sativa* L.
37. *Phlox hoodii* Rich.
38. *Plantago purshii* R. & S.
39. *Psoralea tenuiflora* Pursh.
40. *Sisymbrium altissimum* L.
41. *Taraxacum officinale* Weber
42. *Viola nuttallii* Pursh.

FORBS:

15. *Festuca idahoensis* Emer
16. *Hordeum jubatum* L.
17. *Koeleria cristata* (L.) Pers.
18. *K. species*
19. *Phleum pratense* L.
20. *Poa sandbergii* Vasey
21. *P. species*
22. *Sporobolus cryptandrus* (Torr.) A. Gray
23. *Stipa comata* Trin. & Rupr.
24. *S. species*
25. *Carex filifolia* Nutt.
26. *C. geyeri* Boott
27. *C. pensylvanica* Lam.
28. *C. species*
29. *Achillea millefolium* L.
30. *Ambrosia psilostachya* DC.
31. *Amorpha canescens* Pursh.
32. *Chrysopsis villosa* (Pursh.) Nutt.
33. *Erodium cicutarium* (L.) L'Her.
34. *Evolvulus nuttallianus* R. & S.
35. *Medicago lupulina* L.
36. *M. sativa* L.
37. *Phlox hoodii* Rich.
38. *Plantago purshii* R. & S.
39. *Psoralea tenuiflora* Pursh.
40. *Sisymbrium altissimum* L.
41. *Taraxacum officinale* Weber
42. *Viola nuttallii* Pursh.

SHRUBS:

33. *Artemisia ludoviciana* Nutt.

TABLE 2.—*Determination of forage losses caused by grasshopper populations on rangeland in the Western United States*¹

Reference	Location	Average amount (mg dry-wt) of vegetation destroyed (consumed and wasted) per day by 1 grasshopper	
Anderson, N. L., and J. C. Wright, 1952	Montana	Population 1	76.0
	do	Population 2	91.0
Hewitt et al., 1976	do	Study 1	26.0
		Study 2	47.3
Morton, F. A., 1936	do		44.0
Morton, F. A., 1939	do		9.0
Nerney, N. J., and A. G. Hamilton, 1966	Wyoming		24.0
Pepper et al., 1951	Arizona		37.0
Pfadt, R. E., 1949b	Montana	Site 1	94.0
		Site 2	55.0
	Wyoming	Density 1	28.2
		Density 2	20.4
		Density 3	23.6
Average for all determinations			44.3

¹ Populations contain both nymphs and adults of several grasshopper species common on rangeland.

TABLE 3.—*Determination of forage losses caused by individual North American grasshopper species*

Reference	Location	Species	Average amount (mg dry-wt) of vegetation destroyed (consumed and wasted) per day by 1 grasshopper
LABORATORY STUDIES			
<i>Nymphs</i>			
Misra, D. M., and L. G. Putnam, 1966	Canada	<i>Camnula pellucida</i>	11.7
Parker, J. R., 1930	United States	<i>Melanoplus sanguinipes</i>	127.9 19.2
<i>Adults</i>			
Misra, D. M., and L. G. Putnam, 1966	Canada	<i>C. pellucida</i>	38.7
Mitchell, J. G., and R. E. Pfadt, 1974	United States	<i>M. sanguinipes</i>	83.0
		<i>M. foedus</i>	150.0
		<i>Aulocara elliotti</i>	143.0
Parker, J. R., 1930	do	<i>M. sanguinipes</i>	42.3
Smith, D. S., 1959	Canada	—do—	17.9 20.3 9.3
Pruess, K. P., 1970	United States	<i>Ageneotettix deorum</i>	14.2 13.6
FIELD STUDIES			
<i>Nymphs</i>			
Misra, D. M., and L. G. Putnam, 1966	Canada	<i>C. pellucida</i>	10.1
Putnam, L. G., 1962	do	do	19.3
		<i>Amphitnorus coloradus</i>	13.1
<i>Adults</i>			
Putnam, L. G., 1962	Canada	<i>C. pellucida</i>	96.0
		<i>A. coloradus</i>	53.0

¹ Determined from averaging amounts consumed at different temperatures.

